

ASPECTS OF REPRODUCTIVE BIOLOGY IN THE SEXUALLY DIMORPHIC SHRUB *MALOSMA LAURINA* (ANACARDIACEAE)

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ABSTRACT

Gender distributions of the dimorphic shrub *Malosma laurina* were studied in a population in Ventura County, California, via assessment of population sex ratio, estimation of phenotypic and functional gender, and analysis of sex expression of individual plants. Reproductive investment was investigated via flower number and biomass as well as its effects on phenology and vegetative growth. The population studied had 30% female shrubs, which departed from a 1:1 ratio by Chi square analysis. Both phenotypic and functional gender measurements of males were less than 2% female, demonstrating *M. laurina* to be functionally dioecious. Varying fruit production was found both among and within male shrubs over three successive seasons, without apparent causal relationships with other factors. Reproductive investment was found to be similar between sex morphs at the individual level, despite heavier flower buds among males. Phenologies of thyrsi (i.e., inflorescences) were synchronous between the sex morphs in both flower and fruit development. Vegetative characters (i.e., branch internodal length and leaf measurements) did not differ between the morphs. These results suggest that the near complete dioecy of *M. laurina* appears to have evolved along the gynodioecy pathway from hermaphroditism toward dioecy.

Key Words: Anacardiaceae, biomass, gender distributions, gynodioecy pathway, *Malosma laurina*, phenology, reproductive investment.

The phenomenon of dimorphic breeding systems in plants has been a subject of considerable interest since the time of Darwin's work, *The Different Forms of Flowers on Plants of the Same Species* (1877). This interest has spurred the compilations of texts by Richards (1986), Lovett Doust and Lovett Doust (1988), and Geber et al. (1999). In addition, many selection models have been offered to propose evolutionary pathways toward dioecy with a variety of factors being selected for (Charnov and Bull 1977; Charlesworth and Charlesworth 1978; Beach 1981; Charnov et al. 1981; Ross 1982; Freeman et al. 1997; Charlesworth 1999; Delph et al. 1999; Geber 1999; Marshall and Ganders 2001). Empirically, a variety of dimorphic conditions have been described in many unrelated taxa around the globe (reviewed by Sakai and Weller 1999). Because of this variety of breeding system evolution among seed plants, Baker (1984) had emphasized the need to examine each case individually. Incidentally, several reports of case studies have appeared in the literature in recent years (e.g., Delph et al. 1999; Bram and Quinn 2000; Olson and Antonovics 2000; Marshall and Ganders 2001; Strittmatter et al. 2002), which help to elucidate the evolutionary histories of the species examined.

One such species that deserves study is *Malosma laurina* (Nutt.) Abrams (laurel sumac, Anacardiaceae), in which the sex morphs have only recently been described as female, male, and andromonoecious (Perlmutter 1998). While the breeding system

of *M. laurina* has been classified as "polygamo-dioecious" (Barkley 1937; Perlmutter 1998), this may not be the most accurate term. Depending on author, the breeding system comprising of females, which are constant in their sex expression and hermaphrodites exhibiting reduced and varying female expression can also be termed "gynodioecious" (Lloyd 1973, 1980; Webb 1979; Wolfe and Schmida 1997) or "subdioecious" (Delph 1990; Sakai and Weller 1999). In this paper such classification is not used, in recognition of the variability of sex expression among andromonoecious individuals that can affect the appearance of a population's composition.

Given the continuity of breeding systems from monomorphic to dimorphic states across species in general (Lloyd 1980; Sakai and Weller 1999) and the variation in female expression among andromonoecious individuals of *M. laurina* in particular (Perlmutter 1998), gender quantification through phenotypic and functional gender estimates can yield a more accurate description of *M. laurina*'s breeding system along the gradient between hermaphroditism and dioecy. Further, while variation of gender expression has been only generally estimated previously (Perlmutter 1998), no quantitative analysis has been conducted to explore causal relationships, such as sex allocation trade-offs within hermaphrodites (Wolfe and Schmida 1997; Geber 1999; Olson and Antonovics 2000) or environmental influence (Lloyd and Bawa 1984) for this species.

This report directly follows my earlier paper (Perlmutter 1998), which describes the sex morphs of *M. laurina*. The objectives of the present study

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were to further investigate how the sex morphs differ from each other and to quantify the variation of female expression both among andromonoecious sumacs and within these individuals over successive reproductive bouts (i.e., their gender distribution). The findings of this study also aim to more accurately describe this species' breeding system in context with evolutionary models. Areas of *M. laurina* reproductive biology examined include: population sex ratio, phenology, reproductive investment, vegetative dimorphism, phenotypic and functional gender estimates, and variation of sex expression among andromonoecious plants.

During the course of the study certain plants originally designated "male" were later found to produce fruit and others termed "andromonoecious" based on floral characteristics never fruited. Following the convention of Lloyd (1973, 1974, 1980; Lloyd and Webb 1977; Hoffmann and Aliende 1984; Delph 1990) the andromonoecious and male sex morphs are here treated together as "male", in recognition of their polleniferous function.

MATERIALS AND METHODS

Study Species

Malosma laurina is a large 2–4 m tall evergreen shrub found on sunny slopes and canyons in coastal sage scrub and chaparral plant communities of southern California, and Baja California, Mexico at elevations 0–1000 m (Munz 1974; Wilken 1993). The genus is monotypic, except for the fossil *M. prelaurina* found in Miocene and Pliocene deposits of southern California (Axelrod 1937, 1950). Flowers of *M. laurina* are small (1 mm), white and borne on dense inflorescences (hereafter "thyrsi" following Barkley [1937]), numbering up to 5600 per thyrsus (personal observation). Laurel sumac is bee-pollinated, producing drupes that dry after ripening and often persist in the canopy for at least one year (personal observation). This species is sexually dimorphic with female shrubs exhibiting flowers with stunted androecia exclusively (Engler 1883; Perlmutter 1998) and male plants having thyrsi with approximately 0–25% perfect flowers among those with reduced gynoecia, which produce an estimated 0–25% fruit per plant (Perlmutter 1998).

Study Site

The laurel sumac population studied lay on a south-facing slope along the Cozy Dell Trail, 2 km from the trailhead at Hwy 33 in the Los Padres National Forest, 4 km NW of Ojai, Ventura County, California, (34°27'N, 119°16'W). Located 2 km from the coast, this area is in the Transition Climate Zone (Bailey 1966), influenced by a mixture of maritime and continental air masses (Hickman 1993). Mean climate data for Ojai from 1961–1990

include annual rainfall of 52.6 cm plus January minimum and August maximum temperatures of 2.6 and 32.2°C, respectively (NOAA 1992). At 460 m elevation the site lay in a mosaic chaparral dominated by *Salvia mellifera* Greene, *S. leucophylla* Greene, *M. laurina*, *Eriogonum fasciculatum* (Benth.) Torr. & A. Gray, *Ceanothus spinosus* Nutt. and *Artemisia californica* Less. Due to the difficulty of navigating through dense chaparral on steep terrain, thirty shrubs were selected for study along the trail and an adjoining firebreak.

Phenology

Beginning May 2001 I tracked the phenology of the 30 shrubs from their initial budding through the end of each individual's reproductive cycle, here defined as when all flowers and/or fruits had dried. Visits were made weekly, recording the phenological stages of thyrsi of each shrub, which were classified into five stages: growing buds, mature buds, open flowers, developing fruits and ripe fruits. Since sumacs have numerous thyrsi per individual, which do not necessarily develop synchronously, I recorded all phenological stages observed per shrub during each visit to better represent each sumac's phenology. Phenograms were produced for each stage and were compared between the morphs. Onset and peak dates of each stage plus flower and fruit development periods were determined and compared. Flower development period (D_{Fi}) is here defined as the number of weeks from the date when buds were first observed to the date when at least 50% of a population is in flower (after Bowers [1996]). Similarly, fruit development period (D_{Fi}) is the number of weeks from first observation of developing fruits until when at least 50% have ripened but not dried.

Sex Ratio

Each sumac was sexed upon selection prior to the 2001 reproductive season by checking for abundant dried fruits from the previous season. Those plants laden with fruits were classified female, and those with few or none were classified male. Considering the small sample size under study ($n = 30$), 26 additional shrubs were sexed in 2002 for a larger population of 56. This larger sample's sex ratio was tested against a 1:1 ratio by Chi square.

Inflorescence Measurements

Just before flowering, one representative (i.e., of average size) thyrsus in the mature bud stage was collected from each study plant, and the following measurements were taken: length, width, fresh weight, and number of buds. The timing of harvest was aimed to minimize loss of fragile flowers or floral parts during handling, which could affect accuracy of measurements. Weights in the field were taken with a Pesola 3 g (Pesola, Switzerland) spring scale. Upon immediate return from the field, 2–4

buds of each collected thyrus were removed and fresh-weighed using a Sartorius GMBH analytical balance (Sartorius, Göttingen, Germany). Although dried weights would be preferred, equipment was not available to obtain consistent dry mass, thus leaving a less accurate measure as an approximation of biomass. I pooled these weights per morph ($n_f = 24$, $n_m = 62$) for comparison testing. Thyrsi were collected and processed again in the same manner when fruits had ripened. In October 2002 I collected and weighed five seeds from one 2001-season thyrus, dried on the canopies of eight females and four males, for further comparison between the two morphs. Means of all variables were tested for sex morph differences by two-tailed Student's t-test.

Reproductive Investment Estimates

I estimated total reproductive biomass invested by each sex morph at the individual level by multiplying the mean budding thyrus weight (pooled from the individual weights collected in the field) by the mean number of thyrsi per shrub (i.e., its thyrus load). Similarly, I estimated the reproductive investment in terms of flowers produced per plant. To calculate a plant's thyrus load, photographs of each sumac were taken when in bloom and thyrsi were counted photometrically, since a physical count of numerous thyrsi on a given canopy of these large shrubs would risk count replication. All visible thyrsi were counted on each photograph to represent one shrub face, then doubled to estimate that of the whole plant. This method assumes even inflorescence distribution over the entire plant canopy as based on previous examinations of other sumacs (personal observation) and does not take into account possible uneven distribution resulting from localized canopy disturbance on the hinter side. Because the hinter side of a given sumac is not always accessible due to the dense chaparral vegetation and/or topography, this method only gives a rough estimate of the plant's true thyrus load.

Phenotypic and Functional Gender Estimates

The phenotypic gender of males is expressed as the proportion of flowers producing fruit, which was calculated from the above shrub flower and fruit numbers estimated in the following manner. On each male-fertile plant the number of fruiting thyrsi was counted in a sample of 20 thyrsi. The proportion of fruiting thyrsi was multiplied by the pooled mean number of counted fruits per sampled thyrus and multiplied again by the estimated number of thyrsi per shrub (see above). A gender plot was generated from these data to illustrate their distribution.

An estimate of functional gender of each plant, expressed as its relative femaleness (G_f), was calculated using a pair of formulae developed by

Lloyd (1980) and used by himself and subsequent workers (Barrett 1992; Maurice et al. 1998; Ramsey and Vaughton 2001):

$$G_i = d_i / (d_i + l_i E)$$

and

$$E = \sum d_i / \sum l_i$$

where d_i is the number of ovules (i.e., fruits) produced by plant i and l_i is the number of polleniferous flowers produced by plant i . An assumption to this calculation is that each polleniferous flower has equal probability to contribute to the next generation as each ovuliferous flower in the population, hence the equivalence factor E of the second equation being a ratio of the two sex functions for the population. Using the estimated flower and fruiting loads of each plant, G_i was calculated for each shrub and averaged for the sample population of males (G_m). The functional gender of females (G_f), which were constant in their sex expression, was 1.0, representing both the individual and population levels.

Male Inconstancy

In addition to the 2001 fruiting assessment (i.e., proportion fruits per flower load as estimated for the above phenotypic gender estimates) of each male, I had recorded assessments of the dried 2000 fruit crop in 2001 and the next year's crop in 2002 to check for temporal changes in sex expression. The three sets of proportion data were arcsine-transformed to normalize for comparison testing (Zar 1984). Single-factor ANOVA was performed on the transformed data sets to test for differences by year.

Vegetative Dimorphism

To determine if the sex morphs differed in vegetative growth, I took two internodal lengths (the distance between the current season's thyrus and the previous year's, thus representing one year's growth) of each plant in 2001. These data were averaged per individual, and I analyzed the averages by sex morph using Student's t-test (two-tailed). In 2002 I measured the length and width of two leaves per plant and similarly tested per sex morph.

Statistical analyses were performed using Excel 2000 (Microsoft 1999) with consultation of Zar (1984). As the data sets were not consistently normal in distribution nor consistently homoscedastic, robust tests were chosen for analysis (i.e., two-tailed Student's t-tests and single-factor ANOVA) (Zar 1984). The level of significance for all statistical tests was set a priori at 0.05.

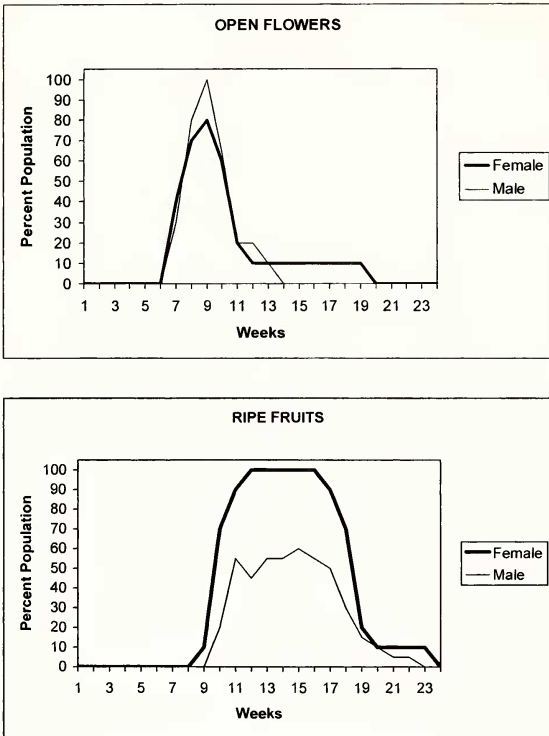


FIG. 1. Phenograms of open flower and ripe fruit stages of male and female *Malosma laurina* shrubs at Cozy Dell Trail, Ventura County, California, 2001. Week 1 began on 6 May.

RESULTS

Phenology

The reproductive season, here defined as from the first emergence of buds to the drying of all fruits, lasted 24 wks, from 6 May through 14 October 2001. Onset and peak dates for all stages measured were synchronous between the sex morphs, differing at most by one week. Flowering began on 17 June and peaked on 1 July (Fig. 1) with $D_{Fl} = 7$ wk for both sex morphs. Fruits began to develop immediately after flowering and were at peak ripeness from mid-July to mid-August (Fig. 1); female $D_{Fr} = 2$ wks and male $D_{Fr} = 3$ wks. Post-peak phenology was less uniform, which resulted from certain plants delaying part of their reproductive efforts due to recovery from localized

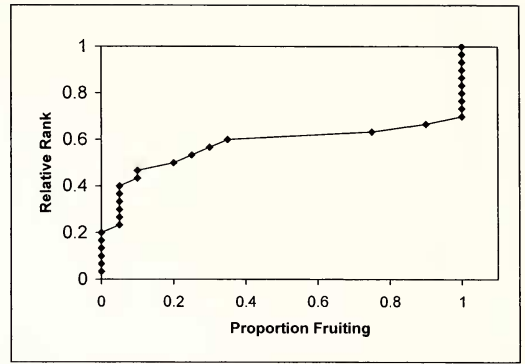


FIG. 2. Distributions of phenotypic gender in males and females of *Malosma laurina* ($n = 30$) in the 2001 reproductive season.

canopy damage, possibly from disease (personal observation).

Sex Ratio

The sex ratio measured in 2002 measured 17:39 female:male plants, or 30% females ($n = 56$). This ratio tested to depart from a 1:1 by Chi square ($\chi^2 = 8.64$, $df = 1$, $P < 0.005$), suggesting a deficiency of females.

Phenotypic and Functional Gender

Six of the 20 male sumacs did not produce any fruit in 2001; among the remaining 14 shrubs proportion of fruiting thyrsi varied from 5–90% (Fig. 2). Altogether, the phenotypic gender was calculated to be 8.0×10^{-5} , or an estimated 0.008% of the flowers on the males produced fruit in 2001. Functionally, males produced 97.47% fewer fruit than females on average (Table 1), which is also reflected in the number of fruits per thyrsus (Table 2). The average $G_{\delta} = 0.011$ for the sample population in 2001, meaning that as a population males contributed only 1.1% of their genes via ovules to the next generation.

Male Inconstancy

Of the 20 male sumacs studied ten produced fruits in 2000, fourteen fruited in 2001 and ten fruited in 2002, with four plants not producing any fruit during the three-year period. As a population

TABLE 1. ESTIMATED REPRODUCTIVE PERFORMANCE OF MALE AND FEMALE SHRUBS OF *MALOSMA LAURINA* AT COZY DELL TRAIL, VENTURA COUNTY, CALIFORNIA, 2001. Numbers in parentheses are one standard deviation.

	Male plants	Female plants
Number plants (a)	20	10
Average no. thyrsi per plant (b)	445.2 (± 331.9)	703.7 (± 535.9)
Average no. flowers per thyrsus (c)	1492.7 (± 1294.5)	937.2 (± 761.4)
Average no. flowers per plant (b \times c)	664 624.7	659 507.6
Average no. fruit per plant (d)	1118.8	529 265.4

TABLE 2. THYRSUS MEAN (\pm SD) DATA AND STUDENT'S T-TEST (TWO-TAILED) RESULTS BETWEEN TEN FEMALE AND TWENTY MALE SHRUBS OF *M. LAURINA* AT COZY DELL TRAIL, VENTURA COUNTY, CALIFORNIA 2001. ^a Not calculated due to influence of dried flowers and drying stalks. * $P < 0.05$, *** $P < 0.001$.

Variable	Female	Male	Student's <i>t</i>
Budding thyrus weight (g)	3.03 (\pm 1.47)	4.70 (\pm 3.32)	1.44
Fresh bud mass (mg)	0.92 (\pm 0.26)	1.86 (\pm 0.80)	4.12***
Fruiting thyrus weight (g)	9.08 (\pm 4.28)	— ^a	— ^a
No. fruits per thyrus	608 (\pm 295)	10.5 (\pm 17.4)	8.77***
Fresh fruit mass (mg)	8.59 (\pm 1.49)	11.68 (\pm 3.50)	2.50*
Dry seed mass (mg)	2.18 (\pm 0.53)	2.85 (\pm 1.04)	1.21

the males did not significantly differ in fruiting from 2000–2002 (single-factor ANOVA, $F = 2.72$, $P = 0.07$). Individual shrubs, however, varied in the amount of fruiting among years in a seemingly random fashion.

Reproductive Investment

Male and female sumacs produced similar numbers of flowers per shrub (Table 1) with similar reproductive biomass investments (i.e., total inflorescence weights) of 2.09 kg and 2.13 kg, respectively. While both morphs produced similar numbers of similarly heavy thyrsi, the mean bud weight from females was half that from males (Table 2). Average fruit weight among male plants was 1.5 times greater than among females. Dry seed weights of males were slightly greater than those of females.

Vegetative Characters

Mean (\pm SD) internodal lengths of the two morphs were 10.1 (\pm 4.1) and 11.8 (\pm 6.8) cm for the female and male plants, respectively. Leaf lengths and widths for female sumacs were 6.5 (\pm 1.1) and 2.9 (\pm 0.4) cm, while those for males were 5.7 (\pm 0.8) and 2.6 (\pm 0.4) cm, respectively. None of these variables differed significantly, although leaves of females were nearly wider (Student's $t = 2.16$, $P = 0.05$).

DISCUSSION

In this study the sex morphs of *Malosma laurina* were found to have synchronous reproductive phenologies and similar vegetative characters. Differences detected include a male-biased sex ratio, plus males having heavier flowers (inferred by bud mass), and far fewer, yet heavier fruits. While not significant, male inflorescences were slightly larger and had more flowers, plus the few seeds that did develop on these plants were slightly heavier than those of females. The gender distributions of the sex morphs revealed *M. laurina* to be functionally dioecious with a very low female expression by male plants. Although this study is from a single population, the patterns observed in Matilija Canyon (Perlmutter 1998), located 9.5 km WNW from the study site, and data from other sites (see below)

support the findings here and together are suggestive for the species.

Phenology

Flowering synchrony between the sex morphs is consistent with other populations in Ventura County (personal observation), but fruiting synchrony appears to be unique to the Cozy Dell population. In Matilija Canyon males fruited 3 wk later (Perlmutter 1998) and in the Santa Monica Mountains (a coastal site in Ventura County near Point Mugu, California) they fruited up to 7 wk later than females (personal observation). Synchronous flowering has been argued to maximize pollination efficiency through poorly selective insects (Hoffmann and Allende 1984) such as bees and flies. Although not quantified in this study, pollinators observed visiting shrubs include European honeybees (*Apis mellifera*) plus occasional native bumble bees (*Bombus* sp.), and hover flies (Diptera: Syrphidae). The differential fruiting phenology found in the three populations could be related to local environmental conditions. Further study is needed.

Sex Ratio

The population studied showed to be 30 percent female. In five populations examined across Santa Barbara, Ventura and Los Angeles counties ($n_i = 19$ –22) in 1996, most also had low female frequencies, ranging 21–58%. Two of these populations tested significant from a 1:1 ratio. While these results suggest a variable pattern of reduced female frequency among laurel sumac populations, caution should be taken in the interpretation of these data due to the small sample sizes. Study of larger populations ($n_i > 100$) is encouraged to confirm this pattern and investigate potential causes.

Gender Estimates

The phenotypic and functional gender results indicate that the *M. laurina* population at the Cozy Dell Trail is functionally dioecious. Populations examined in 1996 ranged 13–63% fruiting among males (i.e., incidence of fruiting per individual), within which the population of the current study lies at 30% at the individual level. Arroyo and Ra-

ven (1975) similarly found near dioecy in two morphologically gynodioecious *Fuchsia* species; less than 10% of hermaphrodites in each species produced fruit, concluding them to be "functionally subdioecious." Lloyd (1980) in his pioneering study using the gender quantification formulae revealed the dimorphic umbel *Gingidia montana* to have phenotypic gender estimates of males to range from 0–92.7% fruiting per individual, and 33.7% fruiting for all males pooled, which is very similar to the this study's results. Functional genders for the female and "male" were $G_{\sigma} = 1.0$ and average $G_{\delta} = 0.23$, respectively. Although more hermaphroditic than *M. laurina* in this study, Lloyd concluded that *G. montana* represents an intermediate stage in the gynodioecy pathway (a theoretical evolutionary pathway from hermaphroditism to dioecy as postulated by Charlesworth and Charlesworth [1978]), with males placed on "average about halfway between equal transmission via pollen and ovules (i.e., hermaphroditism) and strict unisexuality." Barrett (1992), who also used Lloyd's formulae, found even greater variation in gender estimates among populations of the Australian geophyte *Wurmbea dioica*. In three populations of *W. dioica* average G_{δ} values ranged from 0.27–0.32 (Ramsey and Vaughton 2001). In comparison with the above case studies this study's findings suggest that the breeding system in *M. laurina* likewise demonstrates the gynodioecy pathway.

Male Inconstancy

No pattern of female expression among males was found in the Cozy Dell population, suggesting this to be nonadaptive developmental noise as described by Lloyd and Bawa (1984). An alternate explanation is differential pollination among individuals, but as bees were observed at all plants regardless of sex expression, this seems unlikely. A lack of sex changing in response to factors such as age or environment is a prediction of the gynodioecy pathway (Freeman et al. 1997), further suggesting *Malosma* to demonstrate this pathway.

Reproductive Investment

The equivalent investments by the morphs in this study could be unique to the Cozy Dell population, as affected by the lack of gender dimorphism found among these plants at the inflorescence level. Flowering thyrsi pooled from six populations ($n_i = 20$) sampled in 1995–1996 across Santa Barbara, Ventura and Los Angeles counties tested longer (6.8 [± 1.3 SD] vs. 5.2 [± 1.4 SD] cm, $t = 4.79$, $P < 0.001$) and wider (9.7 [± 2.2 SD] vs. 7.8 [± 2.3 SD] cm, $t = 2.99$, $P < 0.001$) on average for the polleniferous morph, which agree with the pattern I had reported for the Matilija Canyon population (Perlmutter 1998). Therefore, males generally made a greater reproductive investment in flower number, although this is not always the case.

Biomass patterns reported here is consistent with that of other dimorphic species (Arroyo and Raven 1975; Kohn 1989; Delph 1990; Barrett 1992; Gehring and Linhart 1993; Hemborg and Karlsson 1999). However, caution should be used in the interpretation of this study's results as biomass obtained from fresh weights may only approximate the differences between morphs due to the influence of potential water content variation. Further, currencies not examined (i.e., nutrient allocation) could yield a more complete view of resource allocation than biomass alone (Hemborg and Karlsson 1999).

The greater weight of fruits from males was unexpected, yet consistent with dry seed weights, although the latter was not significant. The greater fruit dimorphism could indicate that more resources were allocated toward fruit tissues among males. A similar pattern is reported for the buffalo gourd, *Cucurbita foetidissima* (Kohn 1989) and a slight trend was observed in seeds of *Wurmbea dioica* populations (Ramsey and Vaughton 2001), although no explanation is offered in either case. Further research is needed to explore potential causes to this pattern.

Vegetative Characters

Branch apical growth and leaf sizes did not differ between females and males, which is not surprising given that reproductive investments of the two morphs were also found to be similar. Differences in life history traits, such as growth, are predicted when one sex invests more than the other toward reproduction (Delph 1999), and many reports have documented dimorphism in these traits (reviewed in Lloyd and Webb 1977). Determination of vegetative dimorphism is encouraged in populations exhibiting greater gender dimorphism (i.e., differential flower loads implied by different inflorescence sizes).

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

In conclusion the sex ratios and gender estimates determined in this study suggest that *Malosma laurina* follows the gynodioecy pathway when compared to patterns reported in other species concluded to demonstrate this pathway. Sexual specialization in this species is nearly complete, with observable gender dimorphism, yet does not seem to extend to vegetative dimorphism, implying that resources are not a limiting factor. While the findings of this study lend insight into the reproductive biology of *M. laurina*, further investigation involving more numerous and larger-sized population samples throughout its range, as well as crossing experiments and seed fertility determinations between the morphs, could confirm and elaborate on the evolution and maintenance of this species' functionally dioecious breeding system.

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